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ORGANS OF CAPTURE IN SOME FUNGI PREYING ON NEMATODES

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In a recent paper in this journal Sherbakoff (**14**) gave an interesting account of a fungus capturing nematodes by insnaring them in ring-shaped structures, later growing into the animals and ultimately consuming them. The ring-shaped structures he interpreted as conidia, and in the absence of any genus known to produce annular spores, he erected a new genus *Anulosporium*, for which he claimed a place near *Helicomyces* Link and *Helicoon* Morgan among the mucedinous Helicosporae. As the merit of the new genus is contingent on the essential character of the annular bodies, whether they really represent or do not represent conidia, it may not be inappropriate to direct attention more particularly to two nema-capturing Hyphomycetes, the brief characterizations and rather meager synoptic illustrations of which might readily be overlooked in the several summaries (**4**, **6**, **7**) dealing with nearly a score of predacious fungi.

The two Hyphomycetes in question produce annular structures which as the figures of them (**4**, *fig. 6, B*; **7**, *fig. 16, B*) indicate are very closely similar in dimensions and in manner of attachment. If the comparison is extended to Sherbakoff's description and photomicrographs (**14**, *pl. 35, A–C, E–G, I–K, N*) of the bodies he interpreted as the conidia of his *Anulosporium nematogenum*, a similarly striking correspondence is evident. In both species the annular structures function in insnaring the nematodes without active or serious constriction, and while rather inconspicuous differences are observable in the initial development within the animals immediately following perforation of the integument, similarity is again evident both in the frequently delayed penetration, and in the somewhat lingering decline of the prey. A doomed animal, often retaining its vigor for some hours after capture, may tear the encircling loop from its slender attachment, frequently to be caught in a second loop, and sometimes following renewed

struggles and a second liberation, even in a third. Sherbakoff's photomicrographs (**14**, *pl. 35, B, J, L 3*) showing two or three annular structures encircling captured animals, testify to a parallelism in predacious habit in the fungus reported by him.

The fact that is of most direct interest here is that the two fungi under consideration produce under favorable conditions conidiophores and conidia of types long recognized. In one of the fungi the conidia are spindle-shaped with rounded ends, measure on an average approximately 47 μ in length and 8.5 μ in diameter, contain mostly 4 and less frequently 5 septa, and are borne in loose capitate arrangement in numbers usually between 3 and 7, terminally on erect conidiophores measuring mostly about 0.3 mm. in height, 3.0 μ in diameter at the base and 1.5 μ in diameter near the tip (**4**, *fig. 6, A*). The principal details of morphology are therefore in tolerable agreement with those attributed to *Dactylaria candida* (Nees) Sacc. (= *Dactylium candidum* Nees) in the general works of Saccardo (**13**, p. 195) and of Lindau (**10**, p. 416), in both of which cognizance is taken of Bonorden's (**3**, *fig. 139*) illustrations in regard to spore septation and also of Oudemans' (**12**) measurements of spore dimensions. Some misgivings concerning the possible identity of the American with the European fungus are aroused in considering the manner of attachment of the conidia, since in my fungus the loose capitate arrangement is brought about by the spores being borne on short terminal spurs, whereas the various figures of *D. candida* show no indication of such modifications at the tip of the sporophore. Yet as the figures of *D. candida* are on a scale of magnification much too small to record such modifications, if any had been present in the material used, without considerable exaggeration, anything like a rigorous interpretation of these illustrations would seem ill-advised. It is hardly necessary to mention, moreover, that the cavalier draughtmanship prevalent in the earlier days of mycology was primarily concerned with the grosser aspects rather than with the more intimate details of external form.

The occurrence of *Dactylaria candida* on the inner surface of bark separated from an old oak stump, as reported by Bonorden (**3**, p. 82), is not at variance with a presumption that it is often or even habitually predacious on nematodes in nature, as I have found

pieces of decaying bark that have been in contact with moist soil a prolific source of many nema-capturing fungi, among the most frequent of these being, indeed, the very one considered probably identical with Nees von Esenbeck's species. Oudemans' discovery on goat dung of the fungus to which he attached the same binomial, provides a circumstance perhaps even more suggestive of a predacious habit, especially as he reported in the same paper, and it may be assumed as a result of similar handling of gross cultures, the occurrence of *Arthrobotrys oligospora* Fres. also on goat dung, and the discovery of his *Monacrosporium elegans* on rabbit dung. The conidium of the latter fungus (**12**, *fig. 9*) shows such an obvious family resemblance to that of one of the species of *Dactylaria* figured earlier (**4**, *fig. 5, A*) as well as to the spores of two of the species of *Monacrosporium* (**6**, *fig. 12, A*; **7**, *fig. 17, A*), that the presumption of a similar biological relationship is difficult to avoid.

From a consideration of morphological similarities and of the character of the substratum in encouraging the multiplication of nematodes, a fair presumption can be entertained that *Monacrosporium subtile*, another fungus described by Oudemans from rabbit dung in the same paper with the species already cited, represents likewise a nema-capturing form. One (**12**, *fig. 10 a*) of the two conidia figured by Oudemans shows at least a moderate resemblance to the conidia produced by the second of the two fungi isolated by me that capture nematodes in delicate, solitary, non-constricting loops (**7**, *fig. 16, B, C*), though because of the pronounced clavate shape of the other spore (**12**, *fig. 10 b*) figured by the Dutch investigator, there would appear to be somewhat greater likelihood of the plants being congeneric rather than conspecific. For the conidia of the American fungus in question are narrowly fusoid, suggesting in shape and septation the macroconidia of various species of *Fusarium*, yet lacking the curious basal modification usual in the latter, and being formed only on discrete conidiophores (**7**, *fig. 16, A*).

As has been mentioned the non-constricting loops or rings present in the fungus provisionally identified as *Dactylaria candida* are so closely similar to those produced by the *Fusarium*-like species of *Monacrosporium* just discussed, that the two plants could not well be distinguished by these structures. Apart from

the very obvious differences in conidiophores and conidia, the former may be recognized by the production individually on delicate stalks, within the substratum, of characteristic globose cells, about 4 or 5 μ in diameter (**4**, *fig. 6, B*), the equivalent of which I have not observed so far on the mycelium of the latter in nematode-infested plate cultures. These cells manifestly correspond to the "globular bodies" described by Sherbakoff for his *Anulosporium nematogenum*, and that with such exactness that specific identity is very strongly suggested. Even if, as seems probable, similar solitary non-constricting loops and similar globose bodies will ultimately be found associated in other nema-capturing fungi—and undoubtedly more than a few of the supposed saprophytes described from excrement of various animals or from decaying plant remains, that are compiled in the "Sylloge fungorum" in such genera as *Arthrobotrys* Corda, *Trichothecium* Link, *Cephalothecium* Corda, *Dactylaria* Sacc., *Dactylella* Grove, *Dactylium* Nees and *Monacrosporium* Oud. will prove to be predacious—it seems doubtful whether a more thoroughgoing agreement will ever be brought to light.

The globose cells which Sherbakoff sets forth as representing an early stage in the development of the annular loops, can, I believe, be more appropriately interpreted as constituting in themselves completed organs of capture, independent of the loops, and designed to take smaller, or in any case, less vigorous prey. In flourishing agar plate cultures of the fungus tentatively identified as *Dactylaria candida*, annular organs can be seen in all stages of development including the earliest stages, but the resemblance of such earliest stages to the globose bodies is certainly not impressive. Again, in the *Fusarium*-like species of *Monacrosporium* similar loops are formed, though globose cells have not been seen associated with them.

The true character of such globose cells would seem revealed in the larger and more robust but otherwise apparently similar structures (**4**, *fig. 7, B*) occurring in a fungus, the solitary conidia of which, typically broadly spindle-shaped and 4-septate, and measuring 30 to 65 μ in length by 13 to 18 μ in diameter, are borne terminally on erect conidiophores approximately 0.2 mm. in height (**4**, *fig. 7, A*). As this fungus was derived frequently from pieces

of rotten wood, a rather satisfactory agreement with *Dactylella ellipsospora* described by Grove (**9**) from England in 1886, prevails with respect to source as well as to morphology of conidiophore and conidium.[1] In any case the globose bodies here are functional in the capture of nematodes in causing them to adhere by means of an adhesive substance, which then soon becomes visible as a cushion-like deposit of transparent, colorless, gelatinous material through the middle of which a narrow process is thrust forth to perforate the animal's integument (**4**, *fig. 7, C*). They correspond well in shape, dimensions and performance, to the subspherical structures described by Zopf (**16**) for his *Monosporidium repens*, which he found abundantly destructive to nematodes in rabbit dung. Either because this nema-capturing fungus of Zopf's failed to produce conidia, or probably because the opaque substratum obscured the organic connection between the conidiophores and the globose bodies, he took the latter to be conidia themselves. Since the German investigator, owing very probably to the greater limitations of the microscopes then available, failed to see the highly transparent adhesive substance by means of which the animals were held fast, his account was phrased in most cautious yet under the circumstances quite justifiably non-committal words: "Merkwurdiger Weise geht, soweit meine Beobachtungen reichen, die Infektion stets von der Conidie aus. Sie legt sich an den Wurm an, ..." None could have realized better than he that the application of a non-detachable globose body, whether conidium or other structure, to an animal as active as a nematode, could not have results very serious for the animal unless in some way the latter was prevented from discontinuing the inimical contact.

It is of historical interest that in failing to see the adhesive substance by means of which the supposed conidia of his *Monosporidium repens* held fast their prey, Zopf missed a clue which might well have led to a truer explanation of the efficacy of the anastomosing hyphal loops of *Arthrobotrys oligospora*. In many cases, to be sure, these loops come to enwrap the struggling nema-

[1] Evidently the same fungus was described later from rabbit dung in Bohemia by Bubak as *Monacrosporium leporinum* (Ann. Myc. **4**: 120–121. 1906).

tode with such evident security that the capture appears purely one of mechanical involvement. In numerous other cases, however, the animal is held very close to its oral region where in many species the forward tapering of the body is so marked that extrication would appear to ensue from even a slight backward movement. Or, again, the body of a captured nematode is in contact with the inner surface of the loop over only a small segment of its circumference, so that the animal can not properly be said to be insnared at all. Examination immediately after the moment of capture ordinarily yields no explanation as to why the violent struggles of the animal should be so ineffectual. After some time, however, a coating of colorless, transparent, mucilaginous material of manifestly strongly adhesive properties becomes visible about the areas of contact between hyphal loop and nematode, and continues to increase in thickness and to spread in extent as the struggles are maintained, until in the end it attains considerable volume.

Although on microscopic examination the anastomosing hyphal loops of *Arthrobotrys oligospora* previous to the capture of nematodes do not reveal any coating of adhesive material, the behavior of the animals in coming in contact with these structures provides excellent indirect evidence that such substance is present. The animals show no alarm or embarrassment in brushing ordinary hyphae as they make their way over the surface of agar plate cultures containing mixtures of various fungi, but on touching a hyphal loop they draw back with a suddenness and violence hardly equalled by a person touching a hot stove with his hand. Through this energetic reflex the animals escape capture, in perhaps nine cases out of ten, so that the enormous numbers that are taken and destroyed daily by the fungus in a petri dish culture yet represent only a relatively small proportion of the encounters that occur between nematodes and organs of capture. As might be expected the same reflex is evident in the behavior of nematodes in agar cultures of the various other fungi in which the apparatus of capture likewise consists in whole or in part of an anastomosing system of hyphal loops produced on the surface of the substratum, and in which colorless transparent adhesive material similarly becomes visible following its effective intervention. Among these fungi are included not only most other forms with 1-septate spores

borne in capitate or loosely capitate arrangement, which even when the arrangement is not repeated at successive nodes, would seem more correctly assignable to *Arthrobotrys* since Matruchot (**11**) and later Elliott (**8**) have shown that the mode of spore formation in *Cephalothecium roseum* Corda (= *Trichothecium roseum* Link), the type species of the genus *Cephalothecium,* is fundamentally different, but also at least one species with swollen, typically 3-septate spores assignable evidently to *Dactylaria* (**4**, *fig. 5, A*) and another with swollen, 3-septate or 4-septate spores (**6**, *fig. 12, A*) which appears eligible for inclusion either in *Monacrosporium* or in *Dactylella.*

As in the fungus last referred to the superficial hyphal loops arise by the development of bridging connections between rather regularly spaced, short, bristling, mostly 2-celled processes (**6**, *fig. 12, B*), which are adhesive more especially on the distal cell, the performance of organs of capture corresponding substantially to the type illustrated by Zopf for his *Monosporidium repens* and to the type exemplified in *Arthrobotrys oligospora* can here be observed side by side. It now becomes apparent that the stubby processes are effective mainly in the capture of the younger, smaller animals, whereas the closed loops by restricting the movements of the prey, and especially by engaging it over a much more extensive adhesive surface, are adapted to hold even the fully grown vigorous adults. It was no mere coincidence therefore that Zopf found his *Monosporidium repens* destructive to "eine auffallend kleine und schmale . . . Anguillulide." Similarly in agar plate cultures captures on the adhesive knob-cells of the probably identical fungus which from the morphology of its conidia would seem the same as *Dactylella ellipsospora,* were found restricted to the smaller individuals of the species of *Rhabditis, Cephalobus* and *Diplogaster* present. The considerably smaller structures represented in the globose cells produced by the fungus provisionally identified as *Dactylaria candida* could therefore hardly be expected to retain any but the smallest larvae, and that perhaps only in the absence locally of firm material providing leverage for the struggling prey. Their usual inefficiency as organs of capture in agar culture media consequently need not imply any lack of effectiveness

in the various materials of far different texture which constitute the field of predacious activity in nature.

Whether adhesive material is present on the solitary non-constricting loops which Sherbakoff interpreted as conidia, remains somewhat uncertain. None has been observed, but as these organs in both of the species known to produce them are formed within the agar instead of on the surface, the increased optical difficulties might possibly account for this failure. Yet altogether apart from considerations based on direct visual evidence, the performance of these organs is not such as to indicate any necessity for prolonged participation by adhesive material. In all cases of capture they soon fit very snugly around the insnared prey, generally, indeed, becoming jammed so tightly on the tapering body of the struggling animal that the integument is noticeably indented at all points along the circumference of contact (**7**, *fig. 16, C*).

The same optical difficulties intervene in the examination of the constricting loops formed in some predacious representatives of the genera *Trichothecium* (**4**, *fig. 10*), *Arthrobotrys* (**6**, *fig. 13*), *Dactylaria* (**6**, *fig. 14*) and *Monacrosporium* (**7**, *fig. 17*). In none of these representatives has adhesive material been observed, and obviously such substance could here be of no possible use except perhaps for a brief period immediately following capture. Once the swelling of the three component cells is under way, the constricting loop reveals itself as a powerful compressing mechanism as remarkable in adaptation to its special function as it is conspicuous among devices employed by carnivorous plants for the impression of unrelenting malevolence it conveys.

In any case, however, the utilization of adhesive material on the organs of many of the nema-capturing Hyphomycetes provides an important parallelism between this group of predacious forms and the various predacious Phycomycetes that have become known, including the two nema-capturing species figured earlier (**4**, *fig. 8;* **6**, *fig. 15*). In these two fungi the adhesive substance is apparently of a different composition from that common to the several Hyphomycetes, as it very soon assumes a deep golden yellow color which makes it very readily visible under the microscope. Its adhesiveness too would seem to be markedly stronger, as in the form bearing large obovoid conidia on tall erect conidiophores (**4**, *fig. 8, A*).

nearly fully grown nematodes are held securely. A bulbous expansion broadly fused to the animal here usually puts into appearance (**4**, *fig. 8, C*), but as its development apparently occurs after capture of the nematode and preceding perforation of the integument, it seems probable that its function may be more directly related to the latter event than to the former. Both in this fungus and in the nema-capturing fungus which appears referable to the genus *Pythium* Pringsh. (**6**, *fig. 15*) external mycelial modification at the time and place of capture is absent or so inconsiderable that one can hardly speak of special organs. The sigillate outline so characteristic of the cushion of adhesive material attaching the prey to the *Pythium* filament is, of course, not to be interpreted as a result of morphological differentiation. It merely indicates rather that the fashioning of the cushion is closely comparable to the fashioning of a wax seal which it simulates, the struggling animal evidently exerting on the mass of plastic adhesive material a pressure analogous to the pressure of a stamp on heated wax. Yellow adhesive material of similar appearance and consistency is effective in the capture of amoebae by a series of unusually delicate Phycomycetes, which as has been set forth, bear distinctive aerial conidia and small intramatrical sexual organs (**5**, *figs. 2–5*).

Possibly the general similarity in manner of taking prey furnishes a slight indication of taxonomic affinity between the delicate amoeba-capturing Phycomycetes and the much sturdier nema-capturing form with large obovoid conidia. That the latter fungus is not a lone representative of its type has recently become evident through the discovery of several undoubtedly congeneric nema-capturing forms, which more frequently come to bear a number of conidia on a conidiophore, following the repeatedly continued growth of the supporting stalk below each successive terminally formed reproductive body. Whether the large non-septate aerial conidia of these forms can be homologized with the submerse and even larger gemmae which Arnaudow (**2**) described as being produced by the aquatic rotifer-capturing *Zoophagus insidians* Somm. remains uncertain for the present. If analogy is not misleading, the diversity in apparatus of capture found among the fairly closely interrelated Hyphomycetes predacious on nematodes would in-

dicate that the production of the somewhat specialized organs of capture in the short adhesive branches described by Sommerstorff (**15**) and by Arnaudow (**1**) in the original accounts of *Z. insidians* and the similarly aquatic, rotifer-capturing *Sommerstorffia spinosa* Arn. respectively, need not preclude relationship to forms without such predacious modifications.

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